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The Antillean Arc and the distribution of neotropical mosses

Claudio Delgadillo M.

Departamento de Botánica, Instituto de Biología, UNAM, Apartado Postal 70-233, 04510 México, D.F. Mexico.

Abstract. The West Indies have strong continental affinities, but the strongest are with South America, not Central America as was once thought. Moss diversity is the result of migration after the Miocene; the patterns of distribution involving the West Indies and South or North America indicate both migration as well as floristic flows through the Antillean Arc. Speciation due to selective pressures in the changing climate of the Pleistocene gave rise to endemic taxa, but paleoendemics may have resulted in a previous archipelago condition.

A recent contribution stated that there were two routes for floristic interchange between North and South America; one of these, Central America, was considered the major floristic connection between them, but the Antillean Arc was also very important in the migration of mosses between those land masses (Delgadillo 1992). This hypothesis was based on the distributional records of neotropical mosses stored in a databank (LATMOSS) and the observation that North and South America share more than 700 species and varieties of neotropical mosses. Because Delgadillo (1992) made only incidental reference to the West Indies moss flora in his interpretation of the floristic similarities between Mexico and Colombia, in this contribution I would like to discuss the role of the Antillean Arc as a possible floristic connection between North and South America and its role in the dispersal of mosses to and from the Antilles.

Moss biogeography in the West Indies has been examined by several authors. Crosby (1969) investigated the distribution and detected strong floristic affinities between the Greater Antilles and Central America; in comparison, the relationships between the Lesser Antilles and Central America were weaker. According to Crosby (1969), endemism in the Greater Antilles is higher than in the Lesser Antilles; the endemic taxa in the former area are more closely related among them although distant relationships toward northern South America are still apparent. According to Duarte (1982) the strong Central American affinities observed by Crosby (1969) in the Greater Antilles are also evident in the

moss flora of Cuba; in the latter endemism reaches 12.2%, a figure that is considered high by Pócs (1988). This last author recognized the major patterns of distribution in the bryophyte flora of Cuba and indicated that the neotropical, Caribbean and Antillean "subendemic" elements prevail in its bryoflora, *i.e.*, the Cuban bryophyte flora is essentially neotropical in character, but its Andean and Guyana Highland elements reflect old links.

Quoting Crum and Steere (1958), Steere (1984, 1985) stated that the moss flora of the West Indies, especially of the Greater Antilles, is more closely related to that of the sandstone and granitic mountains of Venezuela, the Guianas and eastern Brazil than to the floras of more calcareous mountains and high plateaus of northern South America, Central America, Mexico and the southern Appalachians of the United States. He indicated (Steere 1985) that there were over 90 species of strong continental affinity in the moss flora of the Hipaniola which, with few exceptions, do not occur elsewhere in the West Indies, but only on the mainland.

Despite previous studies, the distribution of moss taxa in the West Indies has not received adequate coverage. Recently, Buck (1990) commented on the historical events that affected moss biogeography in the Greater Antilles. He distinguished between dispersal and vicariance events and referred to the continued controversy on these concepts as applied to Caribbean biogeography. In this contribution, I share Buck's view that while vicariance events may explain the distribution of certain moss taxa, most floristic similarities between the West Indies and North or South America are the result of dispersal. With this in mind, the second objective of this contribution is to review and comment on previous knowledge on the distribution of West Indian mosses.

Method

The relationships of the West Indian moss flora to the Americas were determined with the aid of LATMOSS, a databank for neotropical mosses compiled from the literature. The reader is referred to Delgadillo (1992) for information on this databank which, at present (November 1992), contains 4119 entries.

Results and discussion

Retrieved data from LATMOSS (Table 1) show that the West Indies, in general, have strong floristic affinities to northern South America and Brazil. This is even more apparent by observing that 75% of the Antillean species are known from mainland South America. There are also close relationships toward North and Central America, but not as strong as toward South America. The same is true for the Greater and Lesser Antilles when their data are viewed separately.

Since the Greater and Lesser Antilles have different geological background (*cf.* Buck 1990), independent analysis of their floristic data should indicate whether those differences are reflected in the continental distribution of their taxa. Table 1 reveals that the relationships between the Lesser Antilles and northern South America are slightly higher than those exhibited by the Greater Antilles, as indicated by percentages from their respective moss floras. Something similar occurs with their relationship toward Brazil, but their overall similarity with South America is not very different. However, the figures in Table 1 only give an idea of the general distribution of the flora relative to the major continental divisions.

A closer look at the data in LATMOSS shows that about 381 West Indian moss taxa are common to both North and South America (Table 2). However, there are groups of taxa restricted to portions of this area, *e.g.*, 60 species are distributed from the West Indies northward, but not present in South America; about 199 occur from the West Indies southward, but are not present in North America. When the data for the Greater Antilles are examined separately, there are 59 species shared with North America and about 139 with South America; the Lesser Antilles share 3 species with North America and 78 with South America.

The statistics in Table 1 and 2 thus confirm the close relationships between the West Indies and South America. The Central American link is, as

Table 1. American distribution of West Indian mosses. Numbers in parentheses are percentages from total moss flora.

AREA	WEST INDIES	GREATER	LESSER
Colombia	368 (48)	333 (50)	133 (55)
Venezuela	330 (43)	294 (44)	139 (57)
Guyana	164 (21)	139 (21)	109 (45)
Suriname	156 (20)	137 (20)	99 (41)
French Guiana	130 (17)	112 (17)	88 (36)
Brazil	392 (51)	341 (51)	161 (66)
South America	**580 (75)**	**500 (75)**	**198 (81)**
E United States	124 (16)	122 (18)	45 (19)
E U.S. not Mex.	18 (2)	16 (2)	3 (1)
Mexico	413 (54)	397 (59)	116 (48)
North America	**441 (57)**	**420 (63)**	**123 (51)**
Central America	**489 (64)**	**454 (68)**	**153 (63)**
Endemic	109 (14)	71 (11)	16 (7)
Total	769	669	243

Table 2. West Indian mosses shared with North and South America.

AREA	Number of species
WEST INDIES and	
North America, not in South America	60
South America, not in North America	199
GREATER ANTILLES and	
North America, not in South America	59
South America, not in North America	139
Lesser Antilles	176
LESSER ANTILLES and	
North America, not in South America	3
South America, not in North America	78
WEST INDIES, NORTH AND SOUTH AMERICA	381

indicated by Crosby (1969), stronger in the Greater Antilles as compared to the Lesser Antilles, but not substantially so. Figures in Tables 1 and 2 do suggest, however, that because there are large numbers of species in common with each major continental division, the mainland may be the most important geographical source of the mosses for the flora of those islands. If dispersal is assumed, the major floristic flow toward the West Indies occurred northward from South America while moss interchange with Central and North America though significant was of secondary importance. Endemism (Table 1) as another source of floristic diversity is not as important as was once thought (*cf.* Crosby 1969).

The floristic exchange with North America was perhaps possible from Mexico, mainly but not exclusively, through the Yucatan Peninsula and from eastern North America through the Peninsula of Florida. The mosses shared between the Greater Antilles and the eastern United States which are not found in Mexico, while small in number, are indicative of this second route of migration.

In addition to the strong South American affinity and in spite of the difference in the size of their moss floras, the Greater and Lesser Antilles maintain close floristic links between them. They share about 176 species and varieties, *i.e.*, nearly 72% of the mosses known from the Lesser Antilles are also found in the Greater Antilles.

The presumed role of the Antillean Arc as one of the two major routes for moss interchange between North and South America is also supported by the high number of mosses common to these areas and to the West Indies. However, because most taxa shared by the three areas are also distributed in Central America, it may be concluded that the Central American bridge as well as the Antillean Arc acted simultaneously in moss migration and that both routes were in operation since Tertiary times (*cf.* Graham 1972). Among the West Indian mosses there are, nevertheless, some species with a narrower range which includes one of the islands and North America (Table 3). I find no evidence in this table of an east-west trend in the number of species found on individual islands, although the very existence of West Indian species distributed in North America (unknown from South America), may denote a dispersal route from the mainland. The same may be said of the species distributed in the eastern United States and the West Indies that are not known from Mexico. It is not improbable to regard some of these patterns as signs of previous wider distributions (*cf.* Table 3), but it is more likely that they represent relatively recent events of dispersal.

The reciprocal pattern, *i.e.*, the West Indian mosses distributed in South America and one of the Antillean islands (Table 4), do not show an east-west trend either. However, it is evident that the species shared with South America are more numerous than those from North America and that the presumed continental affinity *sensu* Steere (1985), has to be revised on the basis of current taxonomic concepts and updated information on the distribution of neotropical mosses. This is not to say that the continental affiliation of the West Indian moss flora is non-existent, but that it has to be re-evaluated. Thus, for instance, although the West Indian moss species in common with North America which are unknown from Central or South America form a small group (Table 5), those shared with South America only, are rather numerous. Table 5 emphasizes the close relationship of the West Indian moss flora to South America and, at the same time, its presumed continental derivation.

Considering the number of species shared with portions of the continent and the geological history of the area, it is difficult to envisage the West Indian moss flora as the product of ancient dispersal or even the result of a widspread flora which has remained in place for eons. The geological data indicate that at least Cuba has remained in the same general area relative to North and Central America since the Upper Eocene, but most of its territory was covered by shallow seas up to the Miocene (Iturralde-Vinent 1988). In addition to its archipelago condition and the late elevation of the mountains, the climatic changes of the Pleistocene must have depleted the extant rafting moss floras so that recent arrivals must have been brought in by dispersal. This may

Table 3. West Indian mosses distributed in North America, restricted in the Antilles to one area, not present in South America.

NORTH AMERICA and	No. Species
Cuba	10
Jamaica	1
Hispaniola	21
Puerto Rico	3
Lesser Antilles	0

Table 4. West Indian mosses distributed in South America, restricted in the Antilles to one area, not present in North America.

SOUTH AMERICA and	No. Species
Cuba	14
Jamaica	5
Hispaniola	28
Puerto Rico	9
Lesser Antilles	33

Table 5. Number of moss species restricted to two areas in the Americas.

WEST INDIES and	Number of species
North America	20
Central America	14
South America	110

explain the high degree of specific community in the moss floras of the islands and between the islands and the continent.

The summary of Pleistocene climatic changes presented by Buck (1990) indicated that sea level has fluctuated dramatically; it dropped *ca.* 120 m during glaciation and was above 8-10 m above present levels during the interglacial, *ca.* 65,000 years ago. Besides a changing land availability, the climatic succession of drier and wetter cycles certainly contributed to depauperate moss floras. Climatic changes were not confined to the Pleistocene and were surely generalized in the entire Caribbean area and the world; mean annual temperatures in Central America and Mexico were 2-3 °C in mid-Pliocene (Graham 1989). The resulting downward shift in the vegetation may have caused the displacement of floras in the West Indies and elsewhere in the Caribbean basin as well as an increasing number of temperate migrants during cooler cycles. The endemic moss taxa are perhaps the end products of these evolutionary pressures. To get a more precise picture of the West Indian bryogeography it may be desirable to study selected taxa from the standpoint of vicariance biogeography. The geological background is ripe (*cf.* Rosen 1985), but we need to know more about distribution and taxonomy of West Indian mosses to attempt further analysis.

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